Does body size of coccinellid predators (Coleoptera: Coccinellidae) influence their preference to eat well-defended prey?

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Abstract:【Aim】Despite the fact that coccinellids display inter- and intra-specific size variations, the question of whether size variations in coccinellid species modify their choice to eat well-defended prey (*i. e.*, displaying various defence responses, including actively evading capture, fighting off predators or frequently using defensive chemicals) is still unclear. In present study, we hypothesized that irrespective of their size the coccinellid predators, *i. e.*, *Coccinella septempunctata* (L.) (C7) and *Menochilus sexmaculatus* (Fab.) (Ms), would increase their consumption of a prey type [*i. e.*, the mustard aphid, *Lipaphis erysimi* (Kaltenbach)] only when prey instars would be well-defended. This is because well-defended prey instars are large and more energetic.【Methods】We therefore, categorized the 4th nymphal instar of *L. erysimi* as well-defended and the 2nd nymphal instar as poorly-defended and assessed their preference by large and small variants of the two coccinellid species.【Results】The results revealed higher consumption of poorly-defended instar nymphs by both female variants of Ms, while large and small females of C7 consumed higher percentage of well-defended and poorly-defended instar nymphs, respectively, on an exclusive diet of well-defended/poorly-defended prey. On a mixed diet, female variants of C7 consumed similar fraction of both the prey instar nymphs, while variants of Ms consumed higher fraction of poorly-defended instar nymphs. While consumption of both prey instar nymphs increased with the increase in size of C7 females, but consumption of only well-defended instar nymphs increased with the increase in size of Ms females.【Conclusion】The results therefore oppose our hypothesis and illustrate that: (i) small coccinellids are more confined to poorly-defended prey instar nymphs while large coccinellids selectively consume well-defended prey instar nymphs; and (ii) within and between coccinellid species, preference for well-defended prey instars increases with the increase in size of predators. Results may be utilized for mass rearing of these coccinellids in laboratories for augmentative biocontrol of mustard aphids.

Key words: *Coccinella septempunctata*; *Menochilus sexmaculatus*; *Lipaphis erysimi*; coccinellids; aphids; biological control; aposematic signals

1 INTRODUCTION

Insect pests advertise their defensive mechanism to natural enemies generally through their size (Gerling *et al.*, 1990; Henry *et al.*, 2009). Their larger instars are more energetic and well-defended (*i. e.*, displaying various defence responses, including actively evading capture, fighting off predators or frequently using defensive chemicals) than the smaller instars (Gerling *et al.*, 1990; Dixon, 2000; Sloggett, 2008a, 2008b). However, studies have shown that insect predators strongly prefer those prey instars that maximize their rates of energetic gain (Gelperin, 1968; Hileman *et al.*, 1994; Sherratt, 2003; Sloggett, 2008a, 2008b; Hodek and Evans, 2012). Thus, predators may include certain larger-sized but well-defended prey in their diet so that they benefit from eating the nutrients and energy that larger-sized and well-defended prey contains, particularly when the predators are hungry or in a poor energetic state.

Understanding how predators make these preferences is important, especially in aphidophagous coccinellids, which are an important group of predatory insects with considerable potential for use as biocontrol agents of insect pests, especially the aphids (Hemiptera: Aphididae) (Hodek and Honek, 1996; Michaud, 2012). The aphids are known to exhibit a wide range of behavioural, chemical and morphological defences (Dixon, 1958, 1985). The behavioural responses include synchronized twitching, kicking, attacking

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with frontal horns, walking away, and dropping from the plant (Dixon, 1958, 1985; Roitberg *et al*., 1979; Arakaki, 1989). Certain aphid species are aposematic and ingest or sequester toxins from their host plants (Rothschild *et al*., 1970; Wink and Witte, 1991). Other aphid species release defensive secretions when attacked (Dixon, 1958, 1985). For example, the aphids may daub large amounts of siphuncular wax onto predator larvae, causing their immobility and eventual starvation (Dixon, 2000). Further, the effectiveness of these defensive tactics is greater in older aphid instars than in the younger instars (Brown, 1974).

Since numerous studies have been dedicated to prey suitability in coccinellids, both in terms of suggesting prey classifications (Hodek, 1962; Mills, 1981; Malcolm, 1992; Hodek and Honek, 1996; Dixon, 2000; Michaud, 2005) and investigating prey suitability (Bilde and Toft, 2001), hardly any emphasis has been paid on whether inter- or intra-specific size variations in a coccinellid species also modify its preference to eat well-defended prey.

Aphidophagous coccinellids show natural intraspecific size variations (within the same sex) under laboratory conditions (even when reared on *ad libitum* aphid prey), and both small and large males/females are found within small and large coccinellid species (Chaudhary *et al*., 2015, 2016). In agricultural fields, different sized variants of a coccinellid species also coexist. Similarly, aphid species also show intraspecific size variations (Chaudhary *et al*., 2015, 2016). The occurrence of discrete intraspecific variants that differ in size and show differential niche use, usually through discrete differences in feeding biology, is termed as resource polymorphism. Thus, resource polymorphism allows variants or life stages of the same species to differentially utilize resources and overcome intra-specific competitions (Dixon, 2000; Chaudhary *et al*., 2016). Therefore, in coccinellids, where different sized conspecific variants coexist, it is relevant to question whether these will also differentially exploit the prey instars.

In the present experiment, we hypothesized that irrespective of their size the coccinellid predators, *i. e*., *Coccinella septempunctata* (L.) and *Menochilus sexmaculatus* (Fab.) [= *Cheilomenes sexmaculata* (Fab.)], would increase their consumption of a prey type [*i. e*., the mustard aphid, *Lipaphis erysimi* (Kaltenbach)] only when the prey instars would be well-defended. This is because the well-defended prey instars are large and more energetic. Hence, while feeding on them the ladybirds may get higher energetic return and they complete their development and reproduction earlier than when feed on poorly-defended prey. Thus, we predicted that the energy content of prey would affect the foraging behaviour of coccinellid predators, and it is likely that in nature these preferences of predators would be influenced by the energetic content of alternative but poorly-defended prey.

Coccinella septempunctata, being of Palearctic origin, is now ubiquitous owing to its euryphagous nature, large size and ecological plasticity in terms of both genetic and phenotypic polymorphisms (Hodek and Michaud, 2008). *Menochilus sexmaculatus* is another aphidophagous coccinellid of Oriental region, small in size but with wide prey range and greater competitive reproductive ability (Agarwala and Yasuda, 2000; Omkar *et al*., 2005). The prey in the present study is the mustard aphid, *L. erysimi* that has been reported to sequester chemicals from its host plant, which contains certain alkaloids that are toxic to many coccinellid species (Hodek, 1956; Okamoto, 1966). Its pungent smell, possibly due to the presence of allyl isothiocyanates, is also responsible for its reduced suitability as a prey for coccinellids (Joshi *et al*., 1999; Noble *et al*., 2002; Omkar *et al*., 2009). However, the experimental coccinellids have been reported earlier to feed on this prey species (Kumar *et al*., 2013). Because of their polyphagous nature, both coccinellids are recognized as effective biocontrol agents and used in aphid management programs. Further, the results would be utilized to mass multiply these coccinellids in laboratories for augmentative biocontrol of mustard aphids.

2 MATERIALS AND METHODS

2.1 Stock maintenance

Adults of *C. septempunctata* (C7; n = 40) and *M. sexmaculatus* (Ms; n = 40) were collected from agricultural farms of Banaras Hindu University, Varanasi, India (25°20′N, 83°0′E), paired and reared in plastic Petri dishes (14.5 cm × 1.5 cm) under constant abiotic conditions (27 ± 2℃ temperature; 65% ± 5% relative humidity; 14L∶10D photoperiod) in Biochemical Oxygen Demand (BOD) Incubator (NSW-152; Narang Scientific Works Pvt. Ltd., New Delhi, India). They were provided with medium-sized instars of *L. erysimi* reared on mustard (*Brassica campestris* Linnaeus) (Brassicaceae). The eggs laid were collected every 24 h and observed for hatching. The neonates obtained were reared individually under the above mentioned abiotic conditions on the same prey as given to parents.

2.2 Experimental design

Ten-day-old unmated females of C7 and Ms were selected from the stock for experiments, because they are more voracious than middle aged and old females (Mishra *et al*., 2012). Since the males and females of Ms do not show well-defined sexual dimorphism. Thus, after completion of experiments, the individuals were allowed to mate, and the data of individuals identified as females were selected for further analysis. Moreover, the unmated females were selected because: (i) mated females might consume their own eggs (egg cannibalism) resulting in a reduced consumption of prey that would lead to an unrealistic estimate of number of prey that can be consumed, and (ii) unmated females are more voracious than mated females (Rhamhalinghan, 1987). The rationale behind using the most voracious stage for experimentation in the present study is that the voracious individuals are generally exploited in aphid management programs.

The variable sized 10-day-old unmated females of C7 and Ms were segregated into two significantly (C7: t-value $= 43.70$; $P < 0.0001$; Ms: t-value $= 13.19$; $P < 0.0001$) different sized groups of small (C7: 29.93 ± 0.20 mg; $n = 40$; Ms: 5.80 ± 0.08 mg; $n = 40$) and large (C7: 41.33 ± 0.28 mg; $n = 40$; Ms: 7.66 ± 1.39 mg; $n = 40$) females (biomass measured using Analytical Balance: RA-200, Roy Electronics, Varanasi, India). The size variations used were natural variants (genetic pattern) and were not induced, because selection for size using food and temperature variations (phenotypic plasticity) might change the outcome of the study (Dixon, 2000; Chaudhary *et al*., 2016). The females were placed individually in plastic Petri dishes (size as above) containing one of the following diets comprised of the mustard aphid, *L. erysimi*: (i) an exclusive diet of 100 well-defended instars (4th/larger instar) for C7 while 30 well-defended instars for Ms; (ii) an exclusive diet of 100 poorly-defended instars (2nd/smaller instars) for C7 while 30 poorly-defended instars for Ms; and (iii) a mixed diet of 50 well-defended and 50 poorly-defended instars for C7 while 15 well-defended and 15 poorly-defended instars for Ms.

The Petri dishes were sealed for the next 12 h and placed in BOD incubator for the evaluation of consumption rates at abiotic conditions similar to that of stock. The arenas were devoid of host plant twigs to prevent rapid growth of aphid instars as well as their reproduction, to keep their numbers constant. Time duration of 12 h was taken to avoid their moulting into advanced stages. After 12 h, the numbers of unconsumed aphid instars per Petri dish were counted and recorded. The percentage of prey consumed was calculated as: [(number of prey consumed × 100)/total number of prey].

Each treatment was conducted in 40 replicates per coccinellid size per coccinellid species, making a total of 160 replicates per diet. Further, prior to the start of the above experiments, a preliminary investigation ($n = 20$ per variant per coccinellid species) was undertaken to ensure that (i) 100 and 30 aphids were sufficient for large/small sized females of C7 and Ms, respectively, and (ii) 12 h was sufficient for aphids to remain alive in the absence of host plant and not moult to advanced stages.

2.3 Statistical analysis

Data were checked for normal distribution using Kolmogorov-Smirnov test for normality and Bartlett's test for homogeneity of variances prior to further analysis. Means were separated using Tukey's test when data were normally distributed and variances were homogeneous.

The percentage of poorly-defended and well-defended instars of prey consumed both individually and within combinations (dependent variables) by large and small sized females of C7 and Ms were subjected to two-way ANOVA, considering predator species, predator size variants per predator species and their interaction as the independent factors. All percentages of data were subjected to arcsine square root transformation prior to two-way ANOVA.

Further, the scattered plot graphs were extrapolated on individual prey and mixed prey diets between: (i) the percentage of prey consumed regressed against the predator size; and (ii) the number of prey consumed regressed against the predator size.

3 RESULTS

3.1 Predator performance on exclusive diet of poorly- or well-defended prey instars

Results of the present study revealed insignificant effect of predator size variants, but significant influence of the predator species and the interaction between both the independent variables, when the predators were fed on an exclusive diet of poorly-defended aphid instars. In contrast, effects of predator species and interaction between both the independent variables were insignificant, and those of predator size variants were significant when the predators were offered an exclusive diet of well-defended aphid instars (Table 1). Tukey's *post hoc* comparison of means exemplified that the percentage consumption of poorly-defended aphid instars was the highest for the small females of Ms, followed by large females of Ms and C7, and the lowest for the small females of C7. In contrast, the percentage consumption of well-defended aphid instars was the highest for the large females of C7, followed by the large females of Ms, and the lowest for the small females of both C7 and Ms. While the large females of C7 were consuming higher percentage of well-defended aphid instars, but their small females were consuming higher percentage of poorly-defended aphid instars over the contrary sized aphids. However, both the large and small females of Ms were consuming higher percentage of poorly-defended aphid instars over the well-defended ones (Fig. 1: A).

3.2 Predator performance on mixed diet of poorly- and well-defended prey instars

Further, the effect of predator species was significant, but those of predator size variants and interaction between both the independent variables were insignificant, when predators selectively consumed poorly-defended aphid instars from the mixed diet of poorly-defended and well-defended aphid prey. However, the effects of all the three independent factors, *viz*. `predator species, predator size variants and their interaction, were significant when the predators selectively consumed the well-defended aphid instars from the mixed diet of poorly-defended and well-defended prey (Table 1). Tukey's *post hoc* comparison of means further exemplified that on a mixed diet, large and small females of C7 consumed similar percentage of poorly-defended/well-defended aphid instars; but their percent prey consumption was higher than the female variants of Ms. However, large females of Ms consumed higher percentage of well-defended aphid instars than their small females (Fig. 1: A).

Table 1 Two-way ANOVA table showing the effect of predator species [interspecific size variation: large species *Coccinella septempunctata* (C7) and small species *Menochilus sexmaculatus* (Ms)] and predator size variants (intraspecific size variation: C7 large and small; Ms large and small) on the percent consumption of prey variants (poorly-defended and well-defended instars) individually or within combination

Variables	Predator species	Predator size variants	Interaction
Poorly-defended prey individually	$F = 24.44$ $P < 0.0001$ $df = 1, 159$	$F = 1.37$ $P = 0.244$ $df = 1, 159$	$F = 5.08$ $P = 0.026$ $df = 1, 159$
Well-defended prey individually	$F = 0.02$ $P = 0.887$ $df = 1, 159$	$F = 34.74$ $P < 0.0001$ $df = 1, 159$	$F = 1.04$ $P = 0.308$ $df = 1, 159$
Poorly-defended prey within combination	$F = 18.74$ $P < 0.0001$ $df = 1, 159$	$F = 0.10$ $P = 0.756$ $df = 1, 159$	$F = 3.65$ $P = 0.058$ $df = 1, 159$
Well-defended prey within combination	$F = 128.56$ $P < 0.0001$ $df = 1, 159$	$F = 8.58$ $P = 0.004$ $df = 1, 159$	$F = 4.42$ $P = 0.037$ $df = 1, 159$

F-values significant ($P < 0.05$).

3.3 Predator-size versus prey-defence relationship

Moreover, the scattered plot graphs on individual and mixed prey diets between the percentage of prey consumed regressed against the predator size revealed a decline in percentage consumption of poorly-defended aphid instars but incline in percentage consumption of well-defended aphid instars with the incline in interspecific predator size. These results further demonstrated increased consumptions of poorly-defended and well-defended aphid instars by small (Ms) and large (C7) predator species, respectively (Fig. 1: B). Further, the scattered plot graphs on both prey diets between the numbers of prey consumed regressed against the predator size revealed a rise in percentage consumption of both poorly-defended and well-defended aphid instars with the increase in size of C7 females (Fig. 2: A). However, the consumption of poorly-defended aphid instars remained constant but those of well-defended aphid instars increased with the increase in size of Ms females (Fig. 2: B).

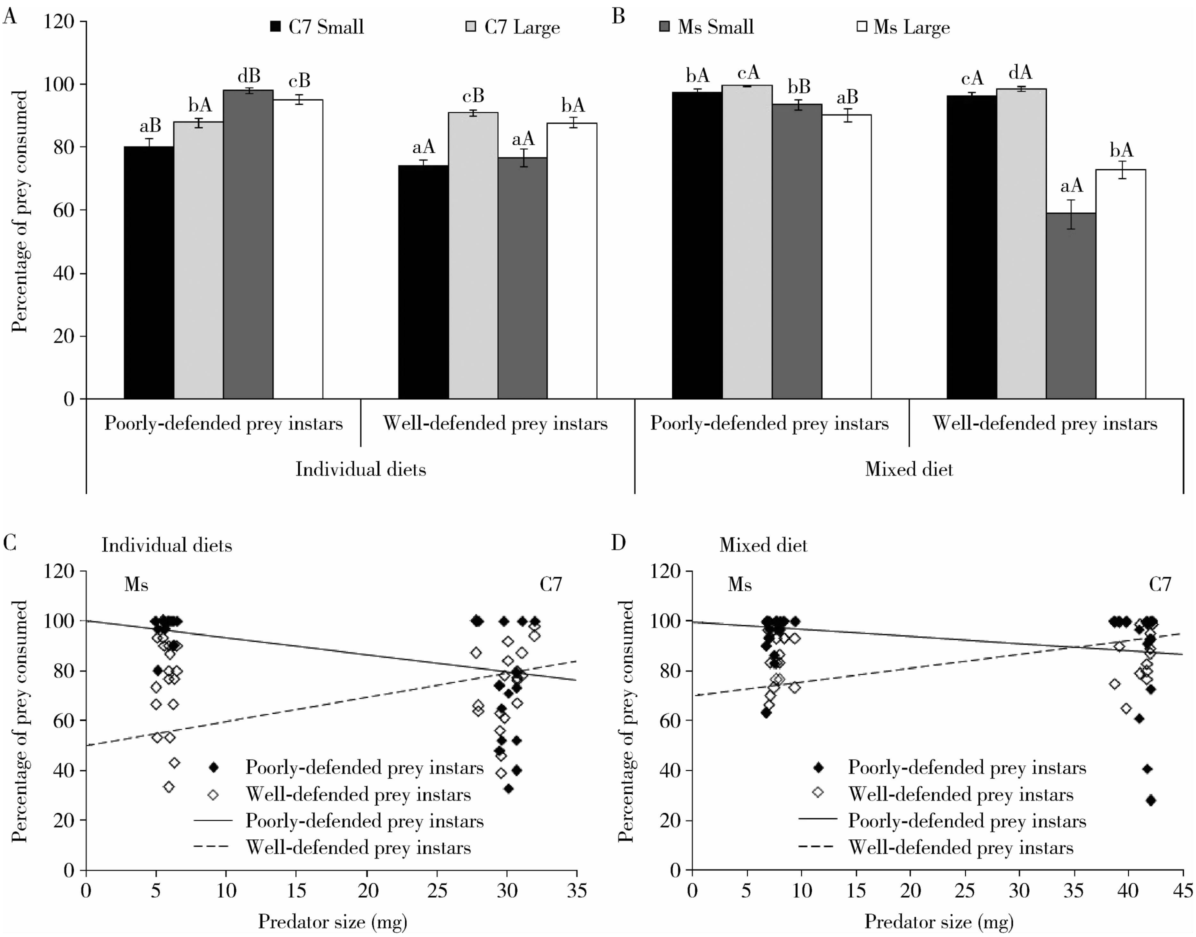

Fig. 1 Percentage of prey consumed by predator species *Coccinella septempunctata* (C7) (A) and *Menochilus sexmaculatus* (Ms) (B) and scatter plot graph showing the effect of the size of predator species on their percent prey consumption, when kept individually on a diet of poorly-defended or well-defended prey instars (C), or their combination (D)

Values are mean ± *SE*; small and large letters represent comparison of means between predator size per prey instar, and between prey instars per predator size, separately on both individual and mixed diets.

4 DISCUSSION

4.1 Predator performance on exclusive diet of poorly- or well-defended prey instars

In the present study, higher consumptions of poorly-defended and well-defended prey instars were recorded for the small females of Ms and large females of C7, respectively. Since Ms is a small while C7 is a large coccinellid species (Mishra *et al.*, 2011, 2012; Kumar *et al.*, 2013; Omkar *et al.*, 2014), this further suggests that the respective small and large coccinellids are more capable of capturing and consuming the smaller/poorly-defended and larger/well-defended prey instars. Such observations are probably owing to: (i) body size constraint in small coccinellids (Dixon, 2000; Sloggett, 2008a, 2008b), and (ii) high energy requirements and metabolic costs of large coccinellids (Sloggett, 2008a, 2008b; Mishra *et al.*, 2011, 2012).

Moreover, the poorly-defended instars of *L. erysimi* are supposed to have poor energy content and display poor defensive responses owing to their small size (Brown, 1974). They may not easily run off from the hold of small coccinellids. In contrast, the large size, high energy content and the ability to sequester more toxic chemicals from their host plants probably allow the well-defended instars of *L. erysimi* to actively evade capture and even fight off small coccinellids. On the other hand they may be restrained by the large coccinellids, which may possibly be capable in metabolizing/detoxifying the allelochemicals that well-defended instars of *L. erysimi* derive from their host plants, as has also been reported earlier (Omkar and James, 2004; Kumar *et al.*, 2013).

Further, while the large females of C7 were consuming higher percentage of well-defended prey instars, their small females were consuming higher percentage of poorly-defended prey instars. Such intraspecific variations in prey consumption by large

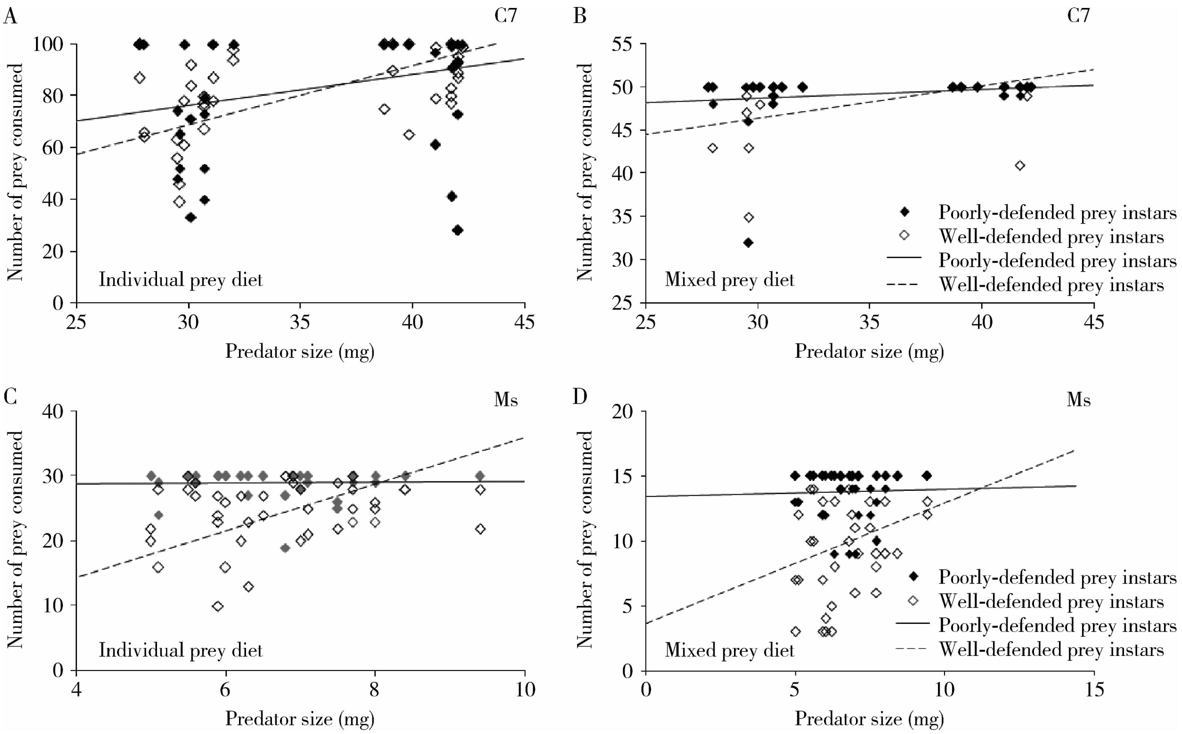

Fig. 2 Scatter plot graph showing the effect of the size of *Coccinella septempunctata* (C7) and *Menochilus sexmaculatus* (Ms) females on their prey consumption, when fed individually on a diet of poorly-defended (small/2nd) or defended (large/4th) prey instars, or their combination

A: C7, individual prey diet; B: C7, mixed prey diet; C: Ms, individual prey diet; D: Ms, mixed prey diet.

and small females of C7 on exclusive diets of the two prey instars may be owing to the high energy demands of large females and the size constraint of small females.

4.2 Predator performance on mixed diet of poorly- and well-defended prey instars

However, on a mixed diet of poorly-defended and well-defended prey instars, both the large and small females of C7 consumed higher but equal percentage of both the prey instars. It therefore appears that on a mixed diet, the relatively low densities of well-defended and poorly-defended prey instars have possibly masked the prey preference of large and small females of C7, respectively. Hence they may have equally preferred both the prey instars to fulfill their basic energy requirements and metabolic costs; and to compensate for their additional loss in energy while searching suitable sized prey instars. However, studies quantifying and discussing relationships between the biomass that predators consumed and the energy they actually gained may provide more detailed results.

In contrast to above, both the large and small females of Ms consumed higher percentage of poorly-defended prey instars over the well-defended ones, both on an exclusive diet of poorly-defended/well-defended prey or on a mixed diet. This further reveals that prey preference is not much regulated by the size variants of the small coccinellid predators and small size may still be a constraint to their prey preference. Thus, both large and small females consume smaller and poorly-defended aphid instars when given a choice of both poorly-defended and well-defended prey variants. Further, despite being specialized to exploit smaller and poorly-defended prey variant, large females still have slightly higher preferences for well-defended aphid instars over the small females, probably because these instars are more energetic. The present findings are in conformity with those reported earlier (Agarwala and Bardhanroy, 1999; Mignault and Brodeur, 2006; Sloggett, 2008a, 2008b; Chaudhary *et al.*, 2015, 2016).

4.3 Predator-size versus prey-defence relationship

Moreover, scattered plot graphs demonstrated increased consumptions of poorly-defended and well-defended aphid instars by small (Ms) and large (C7) predator species, respectively. Such findings may be owing to the increased voracity and higher energy demands of large predators with the further increase in body size, as also suggested by Mishra *et al.* (2011, 2012). Further, the percent consumption of both poorly-defended and well-defended prey instars increased with the increase in size of C7 females. On the contrary, percent consumption of only well-defended prey instars increased with the increase in size of Ms females. These findings therefore suggest that probably the preference for well-defended instars increases when either the body size of predator species (interspecific) or the body size of variants of a predator species (interspecific) increases. Consequently, it seems that even on aposematic prey, both resource partitioning and size based resource polymorphism may be present in coccinellids due to existence of size polymorphism, both between species and within the same sex of a species. They not only facilitate large/small coccinellid species or their large/small variants to exploit different prey, but also help them to exploit instars of suitable size and coexist within the same community.

The results of the present study therefore oppose our hypothesis, because we hypothesized that irrespective of their size the coccinellid predators would increase their ingestion of a prey type when prey instars are well-defended rather than poorly-defended. Results however illustrate that: (i) small coccinellids are more confined to poorly-defended prey instars while large coccinellids selectively consume well-defended prey instars, and (ii) within and between predator species, preference for well-defended prey instars increases with an increase in size of predator. The results of the present study may be further tested in other coccinellid species to corroborate the present findings. Moreover, field-based studies are still needed to strengthen the present results.

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捕食性瓢虫的体型大小影响其偏好捕食防御性强的猎物吗?

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摘要:【目的】尽管瓢虫表现出种间和种内特异性体型大小的变异,但是瓢虫体型大小的变异是否会改变其选择捕食防御性强(即表现出各种防御反应,包括积极躲避捕食、挣脱捕食者或频繁利用防御性化学物质)的猎物,这一问题尚不清楚。本研究中,我们假设不论体型大小,捕食性瓢虫七星瓢虫 *Coccinella septempunctata* (L.)和六斑月瓢虫 *Menochilus sexmaculatus* (Fab.)都将增加其对猎物萝卜蚜 *Lipaphis erysimi* (Kaltenbach)的捕食,只要猎物处于防御性强的龄期,原因是处于防御性强的龄期的猎物体型大且更有活力。【方法】我们将萝卜蚜4龄若虫期作为防御性强的龄期,将2龄若虫期作为防御性弱的龄期,评价七星瓢虫和六斑月瓢虫这两种瓢虫的大型和小型变异体对萝卜蚜的偏好性。【结果】结果表明,六斑月瓢虫的大型和小型雌性变异体更多地捕食防御性弱的萝卜蚜,而七星瓢虫的大型和小型雌性变异体分别对防御性强和防御性弱的萝卜蚜捕食较多。在混合饲料上,七星瓢虫雌性变异体对两类蚜虫的捕食百分比相似,而六斑月瓢虫变异体对防御性弱的萝卜蚜的捕食百分比较高。尽管随着七星瓢虫雌虫体型的增大而对两类猎物的捕食增多,但随着六斑月瓢虫雌虫体型的增大,只对防御性强的蚜虫的捕食量增加。【结论】本研究结果与我们的假设相反,并证明了:(1)小型瓢虫更多地只是捕食防御性弱的猎物,而大型瓢虫选择性地捕食防御性强的猎物;(2)在瓢虫种内和种间,随着捕食者体型的增大,对防御性强的猎物的偏好性增加。可将这些结果用于瓢虫的室内大规模饲养,以提高对萝卜蚜的生物防治。

关键词: 七星瓢虫; 六斑月瓢虫; 萝卜蚜; 瓢虫; 蚜虫; 生物防治; 警戒信号

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